DEATH-FEIGNING IN TERRESTRIAL AMPHIPODS.[1]

S. J. HOLMES.

The instinct of feigning death is extensively distributed throughout the animal kingdom and appears to have arisen sporadically in several groups of animals. It crops out here and there among unrelated forms in such a manner that it is evident that the instinct has arisen independently along many different lines of descent. Various theories of the origin of this instinct have been advanced, but it is by no means evident that the method of its development has been in all cases the same. While at Wood's Hole, Mass., during the past summer my attention was drawn to the death-feigning of the large terrestrial amphipods which occur there in great numbers on the beach, and I was led to study the behavior of these animals with the end of ascertaining, if possible, how their peculiar instinct may have arisen. The family Orchestiidæ, to which the terrestial Amphipoda belong, is partly terrestrial and partly aquatic, and the terrestial forms are, as a rule, confined to within a short distance of the seashore where they live in an atmosphere heavily charged with moisture. The instincts of the terrestrial Orchestiidæ which adapt them to their peculiar habitat must have arisen through certain modifications of the behavior of their aquatic relatives; and as there are several terrestrial and two aquatic species of this family found at Wood's Hole the attempt was made to gain light upon the problem by a comparative study of the behavior of these different forms. I was unable to study the behavior of one of the large sand-fleas, *Talorchestia megalophthalma*, as I failed to obtain any specimens in a living condition. The allied species *T. longicornis* is much more abundant at Wood's Hole and may easily be obtained in any desired quantity. It is the only species observed in which the death-feigning instinct is clearly shown, but the other species, as will appear below, manifest the same fundamental peculiarity, though in an altered form.

[1] From the Zoölogical Department of the University of Michigan, Ann Arbor, Mich.

Talorchestia longicornis during the day lies curled up in burrows in the sand situated usually a short distance above high-tide mark where the sand is loose and dry on the surface but moist an inch or more below. The animal remains all day in an apparent stupor much like the sleep of higher animals. The feeding time is at night when *Talorchestias* come out of their holes in swarms and run or hop in a lively manner over the sea-weed near the water's edge. When dug out of its burrows in the daytime *Talorchestia* may lie curled up in its original position, apparently unawakened by the disturbance. Frequently it will make a few hops in the sand and then curl up and lie perfectly quiet. In assuming this condition the body is not only strongly flexed but the legs are drawn up and the antennæ are bent under the thorax, the whole animal assuming as compact a form as possible. While in this attitude *Talorchestia* may be rolled about, picked up and handled, often with considerable roughness, without betraying any signs of animation. It feigns death as perfectly as many of the insects or spiders. After lying in the death-feigning attitude for some time the animal quickly jumps up and scampers away. Waking up, however, is not instantaneous, but is preceded by certain symptoms which may readily be observed if the creature is closely watched. There is first a nervous twitch here and there, then a slight unbending of the antennæ and a straightening of the legs and body—all of which indicate a slight relaxation of the muscular tension under which the animal labors—and finally a sudden spring and attempt to escape. The animal may be induced to feign death by holding it quiet for a moment in the hand or by placing it in the sand. It will feign death many times in immediate succession but the duration of the response becomes on the average less the more often it is caused to repeat the performance. After *Talorchestia* feigns death several times it is more difficult to bring about the response. As it becomes exhausted the death-feigning attitudes become less typical and the body more relaxed and flaccid. The animal is by no means passive while exhibiting this instinct but is in a state of muscular tension; and this condition is, I believe, very common in the death-feigning of other animals. The contact of solid bodies apparently favors the continuation of the

feint; at least the duration of the feint is increased when the body of the animal is surrounded with sand or small stones. This fact was determined by placing *Talorchestias* which had feigned death upon a flat surface and counting the number of seconds the feint continued and then comparing the series of observations thus obtained with an equal number of observations made upon specimens partly covered with sand or small stones. Fifty trials were made and the average duration of the feint of the specimens partly surrounded by sand or small stones was found to be much longer than that of the specimens lying on a flat surface. As *Talorchestia* is coming out of its feint a slight pressure or contact causes it to resume feigning.

There is little evidence that the death-feigning of *Talorchestia* is in any way connected with a conscious attempt at deception. Such a performance is utterly beyond what the degree of psychic development which the Amphipoda have probably attained would lead us to expect. The instinctive action of *Talorchestia* which seems most like an intelligent attempt to deceive an enemy is that of crouching upon the approach of a threatening object. *Talorchestia* when running away often crouches to the ground and lies perfectly quiet if a large object draws suddenly near. When things in its environment become quiet again the animal moves on. *Talorchestia* does not feign death upon receiving purely visual impressions; it requires contact of some sort to elicit this form of response. The same fact seems to be quite general in the death-feigning of animals, especially below the vertebrates, and it is a circumstance, I believe, of considerable significance in relation to our views of the genesis of this instinct.

The value of the death-feigning instinct in *Talorchestia* is obvious. When the animal is dug out of the sand its large size would render it an easy prey to an active bird or mammal if it attempted to seek safety in flight; by lying quiet it is, as every one knows who has dug these creatures out, very easily overlooked on account of the resemblance of its color to that of the sand around it. Its death-feigning and its protective coloration both make for concealment and consequently are of service in the life-history of the animal.

The smaller sand-fleas *Orchestia palustris* and *O. agilis*, live

in a different situation on the beach from that occupied by the the species of *Talorchestia*. The little *O. agilis* is found in countless numbers beneath the piles of seaweed near the water's edge. This species, as its name implies, is exceedingly active. When disturbed it jumps very rapidly and to such lengths that capturing the creature is an exceedingly difficult undertaking. An enemy which could easily catch the large *Talorchestias* would find the attempt to capture *O. agilis* an unprofitable pursuit. *O. agilis* generally continues hopping until it alights in a place where it can readily get under some object or wedge itself between bodies, so that it secures contact on a considerable surface of its body. Contact seems to exercise a peculiar influence upon this organism, a sort of hypnotic effect apparently, which induces it to flex its body, bend the antennæ downward and lie quiet. The body and antennæ are not so strongly flexed as in the death-feigning of *Talorchestia*, but the same actions are performed though not carried so far. When lying thus *O. agilis* may be disturbed slightly without performing any movement, but an attempt to pick it up or push it about will cause it to quickly "come to" and hop away in the most lively manner. This instinct of *O. agilis* to get into close contact with solid objects is an expression of the strong thigmotactic tendency found among amphipods in general. It is a tendency especially marked in the aquatic representative of the Orchestiidæ, *Allorchestes littoralis*. This species is commonly found under or among stones quite high up on the beach above the range of any of the other aquatic species, thereby showing an approach toward a terrestrial habit. When taken out of the water it is able to perform the exceptional feat of walking upright without falling upon its side, although this is accomplished with some difficulty, and of making leaps into the air like its terrestial relatives. When disturbed it usually moves away by gliding on its side, a movement very common among amphipods which is performed by alternately flexing and extending the abdomen. The efforts are continued until they bring the creature into some niche or crevice where the contact sought for is obtained; then it curls up and lies quiet. The thigmotactic reactions of amphipods keep these animals among the seaweeds and rocks where they secure protection and obtain

food. The behavior of the terrestrial *O. agilis* in relation to solid objects is little modified beyond that of the aquatic species. The thigmotaxis of this form is certainly protective in function, not only by enabling the animal to escape detection by lying quiet, but by leading it into situations such as under stones or into crevices which are inaccessible to its enemies.

The behavior of *Orchestia palustris* shows an interesting connection between that of *Talorchestia* and *O. agilis*. *O. palustris* is considerably larger than *agilis* and is not so active in its movements. It is often found in marshes some distance from the seashore. It usually endeavors to escape by running away and resorts to hopping only under necessity. The tendency to get under or between objects is as strongly developed in this species as in *agilis*, and contact has apparently a stronger quieting effect upon it. When lying quiet *O. palustris* may be poked about more or less without being aroused from its thigmotactic lethargy. Only rarely, however, can it be picked up without its making efforts to escape, although it is much less responsive than *O. agilis*. The conduct of this species is intermediate between the thigmotactic response of *agilis* and the death-feigning of *Talorchestia*. Some specimens might almost be said to possess a death-feigning instinct. The curling up of the body and the bending of the antennæ are not carried so far as in *Talorchestia*, but the same actions are performed which, if carried out in a more decided manner and persisted in longer, would result in what would commonly be called feigning death. The death-feigning instinct of *Talorchestia* is an instinct which, I believe, has its root in the thigmotactic responses common among other amphipods. One may easily conceive that by the selection generation after generation of those individuals of *O. agilis* in which the thigmotaxis is most persistent and in which the body is drawn up in the most compact form during the response a mode of behavior like the death-feigning instinct of *Talorchestia* might readily be produced.

It seems not improbable that an instinct having its phyletic root in a simple thigmotactic response may in course of time come to be comparatively independent of contact stimuli. The persistence of death-feigning in *Talorchestia* depends far less upon contact than the thigmotactic reactions of the aquatic Am-

phipoda, although, as has been pointed out above, contact still increases the duration of the feint. Contact, finally, may come to be necessary only to set up the instinctive response, having become entirely superfluous for its continuation. And if we conceive the necessary stimulus to be reduced to a single tap or even a jar we can understand how death-feigning reactions such as are found in certain beetles where the response often follows upon the slightest disturbance may have been evolved. Whether they have been so evolved is a question which it would be rash with the evidence in hand to attempt to answer. The singular circumstance that the death-feigning reaction is almost always evoked in response to some form of contact stimulus might be urged in support of such view. The instinct of feigning death has been evolved independently so many times that it is quite possible, if not probable, that it has risen by different methods in different groups of animals. The problem can be solved only by a careful comparative study of death-feigning in several related forms among the various groups of the animal kingdom in which the instinct occurs.